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## STUDIES ON THE PLANT CELL.—I.

BRADLEY MOORE DAVIS.

### INTRODUCTION.

THIS is the first of a series of papers that will follow one another in the pages of the *American Naturalist*. They will describe the chief structures in plant cells and the most important events in their life histories, largely from the point of view of the morphologist and student of developmental processes. Research upon the plant cell has entirely outrun the general accounts that may be found in several botanical text books and in certain works of prominent zoölogists. We shall attempt to give a general survey of the subject in its present state with references to the most important papers; but this is not to be an exhaustive account of a literature that is already very large and which can probably be treated far more satisfactorily several years from now when it has passed through the criticism that time will give in a field of very active botanical investigation.

American botanists have reason to be proud of the achievements of their countrymen in research upon the morphology and physiology of the plant cell, for much of the best work of recent years has come from them. This in itself has been a great stimulus to the writer to prepare these brief accounts which he hopes will assist the general botanist to a clearer understanding of the progress in this field. They will also serve to contrast the protoplasmic activities among plants with those of the animal cell which has been so well treated in several foreign works and in English by Wilson's *The Cell in Development and Inheritance*.

The author will feel especially gratified if these papers should help to change an attitude towards investigations on the plant cell that is unfortunately too prevalent among botanists. There is a tendency to regard cell studies as a very special field of botanical research with elaborate technique which the average

botanist cannot be expected to master. Those who work in this field are considered as in a department by themselves and are labeled cytologists which is sometimes given as an excuse for knowing little about their results. Cell studies are nothing more than morphological and physiological investigations which are frequently so broad as to break the mould of the narrower morphology and physiology of former years. Cell studies must be the foundation of all exhaustive work in morphology and physiology. Indeed among the lower plants they constitute almost all there is to morphology and will determine the classification and relationships of great groups. There are no better illustrations of this fact than the effect of Prof. Harper's investigations on the ascus and sporangium upon Brefeld's theory of the origin of the Ascomycetes. And again the results of several investigators upon the multinucleate gametes found among the Phycomycetes and Ascomycetes are of the utmost importance to a correct understanding of the phylogeny of these groups. When students of the plant cell refuse to accept the stamp of cytologist and insist and show that their work is simply fundamental morphology and physiology we shall break away from a past that should be outgrown.

The material of these papers will be treated under the following heads.

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## LITERATURE ON THE PLANT CELL.

Reference to special papers will be given by the authors name and the date of publication through lists presented at the end of every section.

There is no comprehensive treatise devoted to the plant cell but the following general accounts and reviews of the literature are important.

1. Strasburger in the *Lehrbuch der Botanik* and Pfeffer in his *Physiology of Plants* present the best general accounts of the structure and activities of the plant cell.

2. Zimmerman in 1893 and '94 ("Beihefte zum Botanischen Centralblatt" vol. 3 and 4), reviewed the literature on the plant cell under the title "Sammel-Referate aus dem Gesamtgebiete der Zellenlehre" and in 1896 collected the literature dealing with the nuclei of plants in a book entitled *Die Morphologie und Physiologie des pflanzlichen Zellkernes*, Jena, 1896.

3. Dangeard discusses a number of cytological topics in the 6th series of *Le Botaniste* (1898) with especial reference to his studies on the Chlamydomonadeae.

4. Fischer, *Fixirung Färbung und Bau des Protoplasmas* Leipzig 1899, presents a critique of the methods of cytological research and the justification of the conclusions based thereon.

5. The most recent analysis of conspicuous activities of the plant cell is that of Strasburger *Ueber Reductionstheilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich*, *Histologische Beiträge* VI, 1900.<sup>1</sup>

## SECTION I. STRUCTURE OF THE PLANT CELL.

It is customary to apply the term cell in Botany not alone to the protoplasmic units of organization but also to the enclosing wall that generally surrounds the protoplasm. Indeed these walls alone when entirely emptied of protoplasm in specialized

<sup>1</sup> To this list should be added an excellent concise review by Koernicke entitled "Der heutige stand der pflanzlichen zellforschung" *Ber. d. deut. bot. Gesell.* 21, (66), 1904. This article appeared too late to be quoted in the earlier papers of this series.

regions of the plant, *e. g.* vascular and certain supporting and tegumentary tissues, are still called cells. When among the lower forms and at certain periods in the life history of many higher plants the protoplasm is naked (*e. g.* zoöspores, sperms, eggs, etc.), these structures are cells in exactly the sense used by zoölogists. We shall consider almost entirely the protoplasmic portion of the plant structure for any extended treatment of the walls would lead us at once into that field of microscopic anatomy termed histology.

### 1. Protoplasmic Contents.

The most highly differentiated region of the cell is the nucleus, a structure remarkably uniform in organization among all plants except the lowest Algæ and some very simple Fungi. These more primitive conditions will be considered in Section VI. Besides the nucleus there are present plastids in all groups except the Fungi. Plastids are likewise specialized protoplasmic elements although much simpler in structure than the nucleus. Nuclei and plastids lie in a protoplasmic matrix called the cytoplasm. Cytoplasm is more variable in structure and activity than any other region of the cell. Thus three forms of protoplasm, nucleoplasm, plastidplasm and cytoplasm comprise all the living material of the cell and may be sharply contrasted with the non-protoplasmic contents, mostly food material and waste products, which will be considered under a separate head. Definite masses of nucleate protoplasm, with or without plastids are termed protoplasts and such are either unicellular organisms themselves or units of a multicellular structure.

#### (a) The Nucleus.

The nucleus is bounded by a delicate membrane that is probably largely or wholly a modification of the surrounding cytoplasm. The nucleoplasm very rarely completely fills the nuclear membrane, the remaining space being occupied by a fluid known as the nuclear sap. The elements in the resting nucleus consist chiefly of material that takes the form of a net work so that the

effect is that of a much coiled and twisted thread whose loops are united at intervals to form large and small meshes. The ground substance of this thread is called linin and imbedded in it as in a matrix are deeply staining granules of chromatin. Chromatin is regarded as the most important substance in the nucleus, chiefly because of its behavior during nuclear division, and in critical periods of the life history of organisms as at sporogenesis, gametogenesis and fertilization (to be described in Section V). Just before nuclear division the chromatin becomes organized into bodies named chromosomes which are remarkably uniform in number and definite in shape for each tissue and period of the plant's life. They will be discussed under "The Events of Nuclear Division" (Section II), and in Sections IV and V.

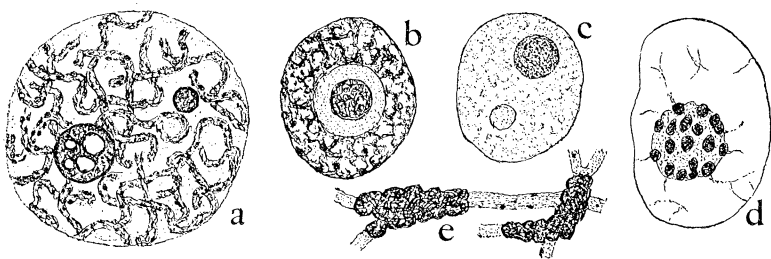


FIG. 1.—The resting nucleus. *a*, Embryo sac of lily with linin thread and two nucleoli. *b*, Root of onion large nucleolus. *c*, Tetraspore of *Corallina* showing large chromatin body and small nucleolus. *d*, *Spirogyra* with central body containing chromatin. *e*, Chromatin on linin net work from egg of pine. After Mitzkewitsch and Chamberlain.

In the meshes of the linin network or lying freely in the nuclear sap may be found one or more bodies, generally globular in form, called nucleoli. (See Fig. 1 *a* and Fig. 1 *b*). The nucleolus is generally regarded as a secretion of the nucleus and it is quite certain that its substance is utilized just previous to and during the period of nuclear division when the spindle is formed. (Strasburger '95 and :00, p. 125, and from the work of others). The structure is not always homogeneous but may show in the interior small vesicles or areas of a different consistency from the periphery. There is often present also a rather thick outer shell or membrane. Sometimes the chromatin in the nucleus may be gathered into a globular body that resembles superficially a nucleolus. Such chromatin bodies are gen-

erally transitory as in *Corallina*, Davis '98, where the structure (Fig. 1 c) is only found in the young daughter nucleus and later fragments into many smaller bodies. In *Spirogyra* however (Moll '94, Mitzkewitsch '98, Van Wisselingh :00, '02) the chromatin is supposed to be always in a globular mass mixed with nucleolar substance and recalls the conditions in certain Protozoa. These chromatic structures however should never be confused with nucleoli, whose substance is different and which are not permanent in the cell, since they may disappear before or during nuclear division and be formed *de novo* in each daughter nucleus.

The substance of the nucleolus is not well understood. It is frequently impossible to distinguish it from chromatin except when favorably situated in the cell and there is much evidence that it is closely related to that substance. In large nuclei of higher plants the chromatin is sometimes gathered into globular bodies without apparent relation to a linin thread and these are readily mistaken for nucleoli and have been called such, but this loose usage of the term should be avoided. And true nucleoli may be so closely associated with the linin net work as to have the appearance of chromatin. Some of these conditions have been especially described by Cavara, '98. Chamberlain, '99, has made a study of the egg nucleus of the Pine where masses of chromatin may take very irregular forms on the linin threads (Fig. 1 c) and sometimes resemble small nucleoli. But such conditions should always be sharply distinguished from true nucleoli which are often caught in the meshes of the linin net work and appear to be a part of it when in reality there are no organic attachments. It is certain that nucleoli are of secondary importance in the cell and probably by-products of the general constructive activities of the nucleus. In which case they may be secretions, perhaps closely related to chromatin, or even direct transformations of this substance. It is well known that the nucleus has wonderful constructive powers, when the amount of chromatin and other nuclear substances may be immensely increased, facts that are especially well illustrated at reproductive periods of the plant's life as during sporogenesis and gametogenesis.

Chromatin is the only substance in the nucleus that is constant



in its presence throughout all periods in every cell's history. It passes on from cell to cell through the mechanism of nuclear division without interruption. There are periods of cell history when the nucleus consists only of chromosomes as in the stages of nuclear division called metaphase and anaphase. The other structures of the nucleus have their relation to definite conditions that are in part understood. The nuclear membrane probably results from the reaction of the cytoplasm to the secretion of nuclear sap among the chromosomes (Lawson, :03  $\alpha$ ). It would then be strictly cytoplasmic in character and similar to the plasma membranes around vacuoles. Nucleoli must be regarded as temporary structures since they generally disappear during nuclear division either dissolving or else passing out into the cytoplasm where they may remain for long periods as deeply staining globules (extra nuclear nucleoli). Linin is believed to be derived from chromatin and in its turn may be transformed into the substance of spindle fibers, which are cytoplasmic, so that chemically it holds a position somewhat intermediate between chromatin and cytoplasm. It seems established that the linin net work is a temporary structure related to the activities of chromatin.

#### (b) The Plastids.

These very interesting structures, characteristic of plant cells, have not received the degree of attention that they deserve and much valuable work may be done in the detailed study of their protoplasmic structure and activities at various periods of ontogeny especially through the series of changes that are presented during developmental processes.

The primitive types of plastids are relatively large structures, often solitary in the cells, and generally of complex form. These are called chromatophores and are characteristic of many algæ especially among the lower groups but are not found above the thallophytes (*Anthoceros* and *Selaginella* excepted).

The chromatophores of the simplest algæ are replaced in most of the higher types of these thallophytes and in all groups above by very much smaller structures, generally discoid in

form, which are called chloroplasts when green, chromoplasts when the color is other than green or leucoplasts if colorless. These plastids are without doubt derived from the more primitive chromatophores.

The colors of chromatophores are various. They are believed always to contain some chlorophyll but this green is frequently so completely masked by other pigments that its presence can only be determined when the additional coloring matters have been extracted. Chloroplasts are universally green except when they may be changing into chromoplasts. Chromoplasts generally take their tint from the predominance of other strong pigments in addition to chlorophyll as phycœrythrin in the red and phyco-phæin in the brown algæ. But chromoplasts may be derived from chloroplasts whose green has largely or wholly disappeared leaving other pigments present as the yellow, xanthophyll, or the orange red, carotin.

The remaining plastids, leucoplasts, are devoid of color and are found in embryonic regions such as eggs, growing points, and in the various tissues of seeds, underground organs and other structures where the cells are largely or wholly removed from sunlight. The leucoplasts may become green upon exposure to light thus changing into chloroplasts. They are responsible for the secretion of reserve starch in many structures (*e. g.* potato) and in consequence have been called amyloplasts.

Leucoplasts, chloroplasts and chromoplasts are morphologically the same structures. It is well known that they may pass one into the other in the order indicated and that chloroplasts and chromoplasts may lose their color and become leucoplasts. It is generally believed that plastids are not formed *de novo*. They divide by constriction and thus multiplying are passed on from cell to cell and it is believed from generation to generation. They are therefore usually ranked as permanent organs of the cell. However, it is but fair to call attention to the fact that there are some serious difficulties in the way of a complete acceptance of these views.

The protoplasmic structure of the plastids of higher plants is rather simple while that of the chromatophores in algæ is more complex since they contain a special organ termed the

pyrenoid. The detailed structure of chromatophores was first described by Schmitz ('82) and of plastids by Meyer ('83). The most complete study of plastids however is that of Schimper ('85). The body of the plastid is always denser than the surrounding cytoplasm. It has a porous structure that is only visible under high magnification and there are sometimes present very delicate fibrils. The coloring matter, oily in consistency, is held in the pores as minute globules. The plastid may therefore be compared to a very fine-textured sponge saturated with pigment. All of the coloring matter of the plastid may be readily extracted with alcohol leaving the colorless proteid matrix.

The pigments of plastids are then in the nature of secretions held in these specialized regions of protoplasm. Chlorophyll is the principal substance and, as has before been said, is almost always present, but the amount is sometimes so small that its green is completely hidden by the color of other pigments. Chlorophyll itself contains greater or less amounts of two other coloring matters that may be readily separated from the pure green, a yellow xanthophyll and an orange red carotin, both substances closely related to chlorophyll. The other pigments, characteristic of the chromatophores in some groups of algæ, are however quite distinct from chlorophyll. There is phycocyan, found in the blue green algæ (Cyanophyceæ), phycophæin and phycoxanthin, characteristic of the brown (Phæophyceæ) and phycærythrin of the red (Rhodophyceæ).

Chloroplasts are found almost universally in green plants above the Thallophytes and are also present in the large group of algæ the Siphonales and in the Charales. They are sometimes formed very numerously in the cell, reproducing rapidly by fission (see Fig. 2 *a* 2, 3) and lie in the layer of protoplasm just inside of the plasma membrane. They are sensitive to light and readily shift their position in the cell. Strong illumination results in their retreat from exposed positions to the sidewalls and bottom of the cell where the light is less intense. If the illumination be weak they may all gather on the side most favorable for the reception of light. These facts are well illustrated by the behavior of the plastids in some of the Siphonales (*c. g.*

Botrydium), in the Rhodophyceæ (*c. g.* Polysiphonia) and also in the palisade cells of leaves. Chloroplasts after exposure to light generally contain starch but in some plants this substance is never formed (*c. g.* *Vaucheria*, Fig. 2 A 1), the first visible products of photosynthesis being other substances more of the nature of oil. It is not known whether the starch grain in the

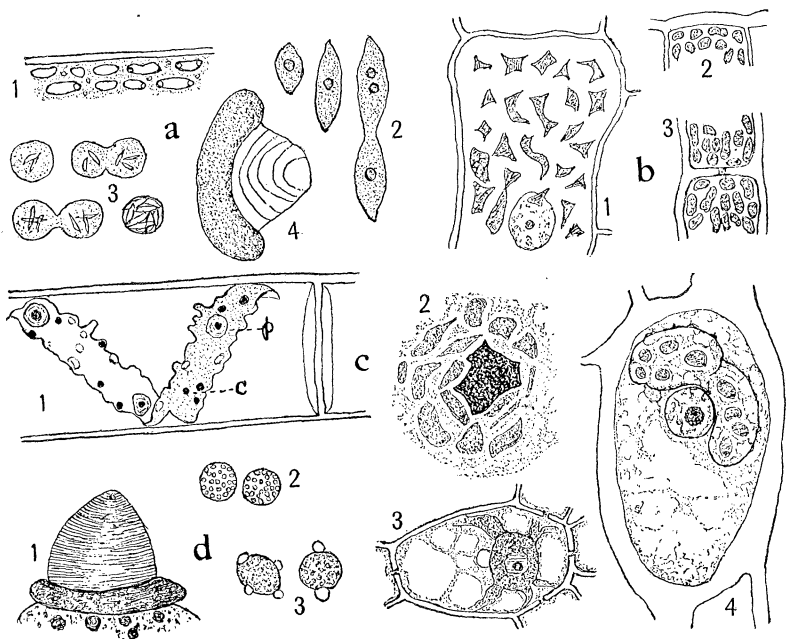


FIG. 2.—Plastids. *a*, Chloroplasts: 1 *Vaucheria*, with oil globules; 2 *Bryopsis*; 3 moss (*Funaria*), in division and containing starch grains; 4 *Oxalis*, with a grain of starch. *b*, Chromoplasts: 1 *Tropaeolum*, epidermal cell from calyx; 2 *Fucus*, 3 *Callithamnion*. *c*, Chromatophores: 1 *Spirogyra*, with pyrenoids (*p*) and caryoids (*c*); 2 *Hydrodictyon*, pyrenoid forming starch; 3 *Nematium*; 4 *Anthoceros*, in division and containing starch. *d*, Leucoplasts: 1 *Phajus*, plastid and starch grain at the side of the nucleus; 2 *Iris*, from root and containing oil globules; 3 *Iris*, in deeper cells of root, with starch grains. After Meyer, Strasburger, P.lla, Timberlake and Schimper.

chloroplast results from the direct change of some of the proteid substance or whether it is a secretion. The conditions are somewhat different when pyrenoids are present in a chromatophore as will be described presently.

The chloroplasts of higher plants may change color under various conditions and become chromoplasts. Some of the best

examples are found in the colored cells of certain floral parts and fruits (Fig. 2, *b* 1). These pigments are generally either xanthophyll (yellowish) or carotin (orange red). Chloroplasts may also turn brown especially in older cells that are losing their contents. The colors of some leaves and flower parts are due not to the plastids but to substances dissolved or otherwise held in the cell sap of the vacuoles. The brilliant coloration of autumn foliage is of this character as well as some of the tints of petals, hairs and other structures. The chromatophores of the higher brown Algæ (Phæophyceæ) and most of the red (Rhodophyceæ) have the discoid form characteristic of chloroplasts (Fig. 2 *b* 2, 3). They might be called phæoplasts and rhodoplasts if one wished to classify plastids according to their color.

The structure of chromatophores is frequently complicated by the presence of pyrenoids which may be quite numerous in the body. These structures are denser regions of the chromatophore with a definite boundary. They are proteid in character and are known to vary in size with nutritive conditions and may completely disappear if the cell is starved. They have been regarded as masses of reserve proteid material but certain functions of great importance are also associated with them. The arrangement of starch grains in the chromatophores of many algæ is clearly around the pyrenoids as centers. For this reason they have been called amyllum centers. Timberlake (:OI) has recently shown in *Hydrodictyon* that segments are split off from the pyrenoids (see Fig. 2, *c* 2) and changed directly into starch grains which naturally lie for a time close to the source of their formation and only later become distributed throughout the chromatophore. It is probable that similar conditions will be found in other algæ (Conjugales, Protococcales, etc.) and we may soon have a much clearer understanding of the pyrenoid. The indications are that the pyrenoid will prove to be a region of the chromatophore differentiated as a metabolic center, more or less prominent according to conditions of nutrition, and that its most conspicuous activity is the formation of starch by the direct transformation of portions of its substance.

Some other structures besides the pyrenoids have been

described by Palla ('94) in the chromatophores of several of the Conjugales and have been named caryoids. Caryoids (Fig. 2, *c* 1) are smaller and more numerous than pyrenoids and are distributed irregularly in the chromatophore but chiefly along the edge. Their function is not known.

The leucoplasts complete the list of plastid structures. They are colorless and may be found in underground or other portions of the plant removed from light or where there is little or no photosynthetic activities as in embryo sacs, seeds, growing points, etc. They become impregnated with chlorophyll under conditions suitable for photosynthesis thus changing into chloroplasts. An important function of the leucoplast is the formation of reserve starch in various parts of the plant. The more recent investigations of this process (Meyer, '95, Salter, '98) claim that it is in the nature of a secretion within the substance of the leucoplast. This view is opposed to the older conceptions (Schimper, '81, Eberdt, '91), which regarded the starch grain as formed by the direct change of proteid material in the plastid. In view of Timberlake's (:01) studies on the pyrenoid of *Hydrodictyon* we may well hesitate to fully accept the views of Meyer and Salter and ask for further investigations of this very difficult subject. In addition to starch leucoplasts may contain proteid crystals and oil globules.

The reproduction of plastids and their evolutionary history in ontogeny and phylogeny offers a very attractive field for research. It is well known that plastids multiply by fission and it is generally believed that they never arise *de novo* but are passed from generation to generation as permanent organs of the cell. The process of division may be very favorably studied in the spore mother-cell of *Anthoceros* (Fig. 2, *c* 4). The fission begins (Davis, '99) by a constriction at the surface as though the bounding membrane of cytoplasm exerted pressure upon an elongating structure. There is no evidence that the interior of the chloroplast undergoes any changes that could assist the process further than a possible tendency of the two separating portions to gather their substance together as division proceeds. The conditions suggest that the division is a mechanical separation of material too bulky for the best advantages of the cell,

for the proper balance of protoplasmic elements in narrow confines, a division prompted by the activities of the cytoplasm rather than emanating from within the plastid.

The view of the permanence of the plastid as a cell organ has received its strongest support from the classical work of Schimper ('85). We are not prepared to deny it and to assert that the plastid may arise *de novo*. Yet those who study the cells of embryonic tissues and reproductive phases know that it is extremely difficult to follow the plastids and that these structures require other than the usual methods of cell research to establish their presence. Several writers (Eberdt, Dangeard, Husek and others) have expressed their belief that plastids may arise *de novo* but no one has thoroughly traced the appearance or disappearance of these structures in any cells.

The plastid in phylogeny has never received the attention that it deserves. Beginning with the conditions among the Cyanophyceæ and the lowest Chlorophyceæ (which will be further discussed in Section VI) we find the pigment distributed so generally throughout the cell that it is doubtful if the term chromatophore should ever be applied to regions so indefinite in outline. Above these groups the pigment is confined to proportionally smaller areas in the cytoplasm and these become chromatophores when their form is clear. The primitive chromatophores were solitary and filled a large part of the cell. The pyrenoids arose in the chromatophores probably as the result of the influence of metabolic centers upon the protoplasm. It is scarcely possible that a large chromatophore should be absolutely homogeneous throughout; there would develop one or more centers of metabolic activity and such would exert some influence on the form of the protoplasm.

But the large single chromatophore does not seem to be the form best adapted to the work of a cell perhaps, if for no other reason, because it requires a mechanical adjustment of other cell organs to itself and would interfere with the quick circulation of material and the general balance of cell activities. It seems possible that mechanical difficulties may have led to the division of large chromatophores and the substitution of numerous small plastids. This change was instituted in the

higher members of the Phæophyceæ and Rhodophyceæ and in the Siphonales, Charales, Cladophoraceæ and some smaller groups of the Chlorophyceæ. The Conjugales whose chromatophores are especially elaborate have cells essentially solitary in their life habits and with a very remarkable adjustment of the cell organs to one another to give almost perfect symmetry. With the splitting up of the chromatophore came the loss of the pyrenoid and the final result was the compact plastid so characteristic of plants above the thallophytes.

(c) Cytoplasm.

There is no region of the plant cell that maintains such varied relations to its environment and performs so many visible activities as the cytoplasm. For this reason the accounts of its structure and behavior have been diverse and there has developed a nomenclature of its parts that is confusing and somewhat difficult to harmonize.

Strasburger has for many years (since 1892) employed the term kinoplasm to distinguish an active portion of the cytoplasm (concerned with the formation of spindle fibers and other fibrillæ, centrospheres, centrosomes, cilia, plasma membranes, etc.) from more passive nutritive regions which he called trophoplasm. Kinoplasm corresponds closely to the archoplasm of the animal cell (Boveri, 1888). This classification has been criticised especially by Pfeffer (:00) on the ground that it employed names signifying physiological differences when the distinctions as far as we know are those of morphology alone. However the physiological behavior of kinoplasm and trophoplasm becomes very real to anyone who studies extensively cell activities and the morphological characters serve to emphasize these peculiarities. The truth seems to be that cell studies cannot be pursued from the standpoint of physiology or morphology alone but must combine these attitudes. And in the union it is hardly possible or perhaps desirable to construct a terminology with strict regard to either field of study. We shall use the terms kinoplasm and trophoplasm grouping the various cytoplasmic structures under these heads.



Cytoplasm has surface contact with three conditions and in each case there is present a delicate plasma membrane, colorless and very finely granular, which is very different in structure from the cytoplasm within. The first of these three membranes is the outer plasma membrane, which bounding the protoplast, is consequently just inside the cell wall. This membrane is called the "hautschicht" by the German botanists, a word for which we have no exact equivalent, the term ectoplast more nearly expressing the meaning than any other but for several reasons not being very satisfactory. Since this outer plasma membrane lies against a moist cell wall it is virtually surrounded by a film of water. The functions of the cell wall in land plants and its developmental history indicate a close relation to the demands of the outer plasma membrane for a fairly uniform environment of moisture, a matter which will be discussed in the last section of these papers.

The second form of plasma membrane surrounds the water vacuoles in the cell. It is very common for the plant cell to have a single large central vacuole containing the cell sap and the membrane around this was named the tonoplast by DeVries in 1885. DeVries believed that this vacuole reproduced itself by fission with each cell division and consequently was a permanent organ of the cell. It is, however, now well known that the large central space containing cell sap is not different from other vacuoles, indeed is frequently formed by the flowing together of several small vacuoles as smaller soap bubbles unite in the froth to form a larger one. A vacuolar plasma membrane is of course bathed by water since it holds the cell sap and its relation to a moist surface is therefore more evident than in the case of the outer plasma membrane.

The third plasma membrane encloses the nuclear sap with the protoplasmic nuclear elements chromatin, linin and the nucleolus. This nuclear membrane was discussed in connection with the nucleus of which it is generally considered a part, but as there stated, the evidence largely indicates that it is cytoplasmic in character, representing a reaction of this protoplasm to the fluid nuclear sap formed around the chromosomes in the daughter nuclei after each division (Lawson :03<sup>a</sup>). The nuclear sap

necessitates the development of a vacuole which becomes bounded by the nuclear membrane. The nuclear membrane in some cases at least differs from a vacuolar membrane in being easily distinguished from the surrounding cytoplasm as a definite film.

The structure of all the plasma membranes is much the same as far as the microscope may determine. The protoplasm is dense, colorless and filled with very minute granules (microsomata). There are no large inclusions such as plastids, particles of food material (starch, proteids, oils, fats, etc.), mineral matter or waste products. These are all held well within the cytoplasm between the outer plasma membrane and the vacuoles. There is good reason to believe that the substance of all plasma membranes is much the same since they perform very similar activities both in relation to the fluids that bathe them and also because their substance in certain cases becomes the protoplasmic basis of cellulose walls. These resemblances are well established for the outer plasma membrane and that which surrounds the vacuoles. Thus, the capillitium of *Myxomycetes* (Strasburger, '84) is formed from the plasma membranes around the vacuoles after the same method as a cell wall from the outer plasma membrane. And again, during cleavage by constriction (see section II) in the plasmodium and sporangium of the molds (Harper, '99 and :00, D. Swingle, :03), vacuoles fuse with cleavage furrows from the outer plasma membrane to form a common membrane which surrounds each spore mass and secretes a wall, thus showing identity of function and structure. The resemblances are less conspicuous for the kinoplasm of the nuclear membrane, only appearing indirectly with certain events of cell division (the formation of the cell plate) which will be discussed in the next section of the paper. The evidence indicates that the three plasma membranes are all kinoplasmic in character, a generalization of some importance since it offers explanations of many peculiar cell activities to be described later.

Since all plasma membranes have these common characters it may well be questioned whether an elaborate terminology is justified for structures so closely related. The terms ectoplast and tonoplast seem undesirable since they were meant to indi-

cate peculiarities of structure and a degree of permanence as cell organs that is not actually present. It seems hardly necessary to define the plasma membranes further than by their position in the cell as the outer, vacuolar and nuclear membranes.

All of the cytoplasm bounded by the plasma membranes with the exception of certain conditions to be described later (centrospheres, centrosomes, asters, filarplasm and blepharoplasts) may be called trophoplasm since it contains structures and substances especially concerned with nutritive functions. Trophoplasm presents an open organization in sharp contrast to the dense kinoplasm. This peculiarity is due in part to numerous small vacuoles which give a spongy appearance to the usual foam like structure and is further complicated by the inclusion of material not strictly a part of the protoplasm in the form of various sized granules. There are sometimes present fibrillæ that impart a somewhat fibrous texture. We cannot discuss here the theories of the structure of protoplasm, which has not been so extensively studied in plants as among animals, further than to point out that it varies considerably in different regions of the cell in relation to peculiarities that will be described later. There is sometimes presented very typically the foam structure of Bütschli but the introduction of small vacuoles generally gives a spongiose appearance. This subject is critically reviewed by Fischer, '99, and has also been treated in several papers of Strasburger especially in '97.

Three well differentiated organs of the cell, probably trophoplasmic in character, require special mention, *viz.*, coenocentra, nematoplasts and physodes. Coenocentra are very interesting protoplasmic centers found in the oogonia of certain cœnocytic fungi among the Saprolegniales and Peronosporales during oogenesis. They appear just previous to the differentiation of the eggs as small bodies sometimes with delicate radiations (see Fig. 3, *a* and 8, *f*), and are found one in each egg origin. They are apt to increase in size as the eggs mature and evidently become the centers of the metabolic activities of the cells, drawing the sexual nuclei into their neighborhood where the latter increase in size (Fig. 3, *a* 2). The cœnocentrum disappears in the ripe oöspore and is consequently an evanescent

structure. It is probably the morphological expression of a dynamic center in the egg. Coenocentra have been known for several years and have been given especial attention in the recent investigations of Stevens, '99 and '01, and the author (Davis, :03). They will be further considered in our account of Cœnogametes (Section III).

Nematoplasts are exceedingly small rod or thread like

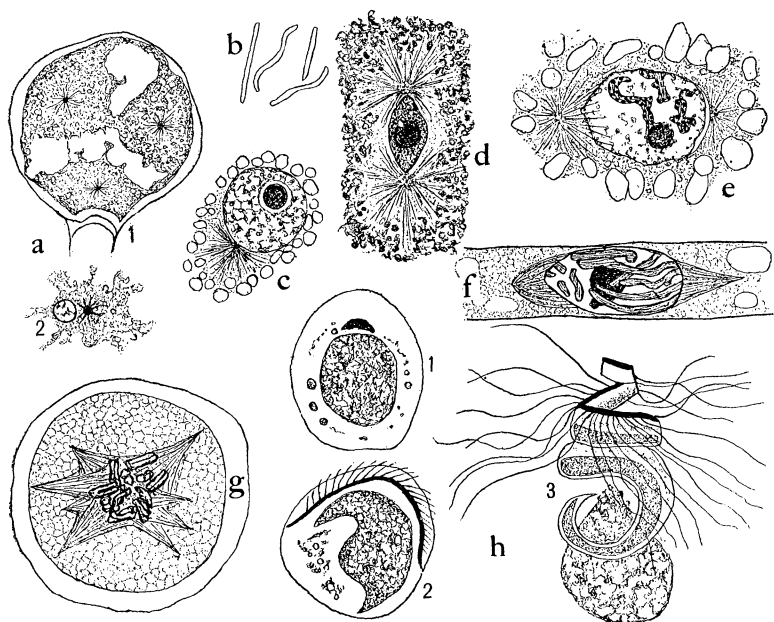


FIG. 3.—Cytoplasmic structures. *a*, Coenocentra of *Saprolegnia*; 1, oögonium, each egg origin with a coenocentrum; 2, coenocentrum and nucleus from mature egg. *b*, Nematoplasts from hair of *Momordica*. *c*, Nucleus from apical cell of *Sphacelaria*, aster with centrosome. *d*, Nucleus from oögonium of *Fucus*, aster with centrosphere. *e*, Nucleus from germinating spore of *Pellia*, centrospheres with short cytoplasmic radiations (aster like). *f*, Nucleus from procambium cell of *Vicia*, kinoplasmic caps. *g*, Pollen mother-cell of *Lilium*, filarplasm in form of multipolar spindle. *h*, Development of sperm of *Gymnogramme*; 1, blepharoplast at side of sperm nucleus; 2, blepharoplast elongating and developing cilia; 3, mature sperm, blepharoplast and nucleus in parallel bands, cytoplasmic vesicle below. After Zimmermann, Hof, and Belajeff.

structures reported by Zimmermann ('93, p. 215) in the cells of hairs of *Momordica* and the root of *Vicia* (see Fig. 3B). It is probable that organs described by Swingle, '98, and Lagerheim, '99, under the names of vibrioides are the same as or closely

related to physodes. Swingle found them in some of the Saprolegniales and certain Rhodophyceæ and Lagerheim in Ascoidea. They are probably not uncommon. Nematoplasts may be proteid crystals but there is evidence that they move, bending slowly back and forth, which suggests a higher degree of organization. They should be further studied.

Physodes are bladder like structures described by Crato, '92, in certain brown Algæ. They contain a highly refractive substance which gives them a very different appearance from vacuoles whose structure they resemble in many respects. Very little is known about the contents of physodes and it may well be questioned whether they are really organs of the cell and not vacuoles set apart to hold some fluids or substances other than cell sap.

There are left for us a group of kinoplasmic structures that are especially prominent and sometimes only present during the events of nuclear division and at the times when cilia are formed. They will be discussed in later sections of these papers. (Sections II, III, V and VI) and at this time we shall give but a brief statement of their appearances. They are centrospheres, centrosomes, asters, filarplasm and blepharoplasts.

Centrospheres are rather large areas of kinoplasm that sometimes lie at the poles of nuclear figures and to which are attached the fibrillæ that form the spindle and also those that may radiate into the surrounding cytoplasm. If the centrosphere contains a distinct central body, or if such a small structure be present alone at the poles of the spindle it is called a centrosome. Should either structure be accompanied by definite fibrillar radiations the whole is termed an aster. These latter conditions are sometimes very complex and are the most interesting types of structures. Asters with centrosomes are known for the brown algæ in the growing points of *Sphacelaria* (Fig. 3c), *Stypocaulon* (Swingle, '97) and the spore mother cell of *Dictyota* (Mottier, :00). They are also beautifully shown in certain diatoms (Lauterborn, principal paper '96, Karsten, :00). Asters with centrospheres and occasionally but not constantly containing centrosome-like bodies are found in the oogonium and germinating eggs of *Fucus*, see Fig. 3, *d* (Strasburger, '97<sup>a</sup>).

Farmer and Williams, '98). Especially well differentiated asters with centrospheres are present during the mitoses in the ascus, functioning at the end in the peculiar process of free cell formation (Harper, '97). Large centrospheres accompanied by radiations are present during the germination of the spores in certain Hepaticæ (Farmer and Reeves, '94, Davis, :01, Chamberlain, :03), but are less conspicuously shown in some and are entirely absent in other phases of the life history. Remarkably large centrospheres with inconspicuous radiations are known in the tetraspore mother cell of *Corallina* (Davis, '98). Centrospheres occur in the basidium (Wager, '94, Maire, :02). Centrosomes have been reported during the mitoses in the sporangium of *Hydrodictyon* (Timberlake, :02). Centrosomes have also been described in other types of the thallophytes but we are justified in asking for further work on these bodies since they are generally without radiations and may not have at all the significance indicated. Neither asters, centrospheres or centrosomes seem to be normally present in groups above the bryophytes, nuclear division taking place in these plants by methods, not found in other organisms, which will be described in succeeding sections.

Vegetative and embryonic tissues of plants above the thallophytes present very different conditions from those described in the foregoing paragraph. The centrosphere is replaced by a less definite structure in the form of a kinoplasmic cap which appears at the ends of the dividing nucleus and determines the poles of the spindle (see Fig. 3, *f*). They have been described in the cells of vegetative points of several pteridophytes and spermatophytes by Rosen, '93, Hof, '98, and Nemec, '99 and :01, and in the seta and late divisions in the germinating spore of the liverwort *Pellia* (Davis, :01).

The most highly developed conditions of spindle formation are found in the spore mother cells of the bryophytes, pteridophytes and spermatophytes. Here the nucleus becomes surrounded by a web of fibrillæ which form a kinoplasmic envelope probably derived in part from the nuclear membrane. The fibrillæ are at first quite independent of one another or of common centers. Most of the fibrillæ enter into the spindle

which may in the beginning have several poles (see Fig. 3, *g*), but these generally swing at last into a common axis so that the spindle finally becomes essentially bipolar. The term *filarplasm* is applied to this free fibrillar condition of kinoplasm without organized centers. *Filarplasm* is peculiar to plant cells and its remarkable activities in connection with multipolar spindles have only been found in groups above the thallophytes. Centrospheres, centrosomes and asters among the lower plants resemble in general the same structures in the animal cell. But *filarplasm* presents a higher form of kinoplasmic structure with perhaps the most complex activities known in the process of spindle formation. We shall consider them especially in Section III when treating the spore mother cell.

The blepharoplasts are in some respects the most complex structures derived from kinoplasm. They are most conspicuous in the sperm cells of higher plants (spermatophytes and pteridophytes) but they are undoubtedly present in lower forms and probably in zoospores. The blepharoplast develops cilia as delicate fibrillæ from its surface. The origin and homologies of the blepharoplast are uncertain. In some forms they resemble centrosomes at the poles of the last nuclear figures in sperm tissue. But in other cases they are entirely independent of such spindles, a character which cannot be brought into harmony with the activities of centrosomes. They finally lie one at the side of each sperm nucleus, see Fig. 3, *h*, and with the development of the sperm they follow the spiral twist, when present, as a parallel band (Fig. 3, *h*, 2 and 3). This structure will receive detailed treatment in our account of the sperm (Section III).

## 2. Non Protoplasmic Contents.

It is not possible to distinguish with certainty all the non-living material of a cell from its protoplasm. We have at one extreme cells from which the protoplasm has almost or wholly disappeared and which are either entirely empty or set apart solely as receptacles for various substances, sometimes waste products and sometimes food materials. In contrast with this

condition are the cells filled with cytoplasm so homogeneous in structure that only the most delicate granules (microsomata) can be distinguished in the clear substance.

Waste products such as mineral matter, resins, certain oils, solutions of tannin and various poisons, such as the alkaloides, may be easily recognized. Most food substances such as starch, proteid grains (aleurone), albumin crystals, oils, fats, etc., are readily separated from the protoplasm in which they lie. But the difficulties are much greater with the smaller particles of proteid material, which are frequently such minute granules as to approach the microsomata in size. These may give to the protoplasm a granular consistency that breaks up the foam or spongiose structure characteristic of the pure condition. These granules are undoubtedly in most cases substances intimately concerned with the metabolism of the cell and are members of the chains of constructive and destructive processes that characterize life phenomena.

The other non protoplasmic structures of cells are vacuoles which are essentially bubbles of fluid lying in the denser protoplasmic medium and surrounded by plasma membranes. The watery fluid of vacuoles contains various substances in solution, carbohydrates such as the sugars glucoses and inulin, mineral salts, asparagin, tannin, alkaloids, etc., and occasionally oil and not infrequently crystals. Vacuoles may be formed in large numbers in protoplasm. They tend to run together as do bubbles in a froth and in this way the large central vacuole becomes established in the cell, gathering to itself many smaller vacuoles until the protoplasm is forced to lie as a relatively thin layer next the cell wall. The fluid in the central vacuole (cell sap) is generally thinner and more watery than that in the smaller vacuoles. The latter are apt to be more rich in albumen which may be transformed into proteid grains as is especially well illustrated in the secretion of aleurone. Cell sap may be colored by pigments in solution and the tints of flowers are largely due to this cause alone or to the effects of its color in combination with various plastids in the cell.

It is possible that physodes, described among the cytoplasmic structures, are in reality vacuoles filled with substances other than cell sap, which are not as yet understood.



### 3. The Cell Wall.

Many of the chief peculiarities of plant organization and activities are due to the presence of the cell wall, its influence on structure and mode of life. The cell wall is not an excretion, from the cell like a mineral shell but is formed by the direct change of portions of the protoplasm. The regions concerned may be the outer plasma membrane, the vacuolar plasma membrane or the substance that makes up the spindle fibers which form the cell plate. These structures are all kinoplasmic in character and have to do with the formation of cell walls in various ways which will be described in Section II under the topic "The Segmentation of the protoplasm." The transformation of finely granular films of kinoplasm into cellulose is not well understood but there is an evident solution of the granules (microsomata) and the change of the resultant substance into the cell wall. As a chemical process this change means the replacement of molecules of an albuminous nature by those of a carbohydrate substance. The most complete account of the cell wall is that of Strasburger, '98.

Cell walls are chiefly composed of cellulose, but other substances are always present, modifying the structure in various ways to give widely different properties. These modifications are generally due to infiltrations of foreign substances but sometimes cell walls become incrustated with mineral deposits. The group of cellulose compounds is very large and it is extremely difficult to identify the various substances in structures so small as the cell walls. For a detailed treatment of the chemistry of the cellulose group the reader is referred to Cross and Bevens, '95, and for a general account to Pfeffer, '00, p. 480-485. There are microchemical tests for cellulose that give good reactions for most tissues but which cannot be relied upon for some walls (as in fungi and many algæ) yet it is well understood that the cell walls of these organisms are from the biological point of view essentially the same as for other plants. The cell walls of some fungi are very largely composed of chitin.

Several substances known to be present in cell walls give them marked characteristics. Their association with the cellu-

lose is so intimate as to resist very severe treatment and therefore these cell walls are essentially cellulose groups modified chiefly in their physical properties by the presence of foreign substances. The most conspicuous modifications of this character are lignification, suberization and cutinization. Lignified walls are permeable to water and gases. Several substances have been separated from the cellulose of lignified walls, among them lignone, coniferin, vanillin, etc. Suberized and cutinized walls are largely but probably never wholly impervious to water and gases; the one is infiltrated with suberin and the other with cutin, substances that resemble one other very closely. Even walls that appear to be pure cellulose have other substance united with them, the most important being pectose and callose. Cell walls frequently become gelatinous or mucilaginous, when the outer layers swell and lose their form or they may be transformed into gums. These changes are well illustrated in the coats of seeds and fruits and among the algæ and fungi. The cells of algæ frequently secrete gelatinous envelopes or sheaths of substances so closely related to cellulose that were they condensed they would form a firm cell wall.

The cell wall may grow in two directions by methods quite different from one another. There is first surface growth which results in a stretching of the cellulose membrane (growth by intussusception). And second there may be growth in thickness by the formation of successive layers of cellulose inside of one another, giving the wall a striated structure (growth by apposition). The second type of growth is chiefly interesting since it makes possible many peculiarities of structure, because the newly formed layers may not be deposited uniformly inside the primary wall. In some cells the secondary thickenings have the form of rings or spirals or a reticulate structure. The reticulate condition passes insensibly into the pitted cell in which the secondary layers cover the greater part of the surface leaving the primary wall only exposed at the pits. Further discussion of these cells falls more within the range of histology than the purposes of this paper.

The cell wall offers a very interesting field of research among the thallophytes and especially in the lower groups where we

may expect to find these envelopes in a fairly primitive condition and may be able to establish the steps in the origin and differentiation of this very important accessory structure to the plant cell.

(To be continued.)

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*(To be continued.)*